Soil Biology and Biochemistry 123 (2018) 180–189

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: www.elsevier.com/locate/soilbio

Interactive effects of warming and nitrogen addition on fine root dynamics of a young subtropical plantation

Decheng Xiong[a,b], Zhijie Yang[a,b], Guangshui Chen[a,b], Xiaofei Liu[a,b], Weisheng Lin[a,b], Jinxue Huang[a], Francis P. Bowles[c], Chengfang Lin[a,b], Jinsheng Xie[a,b], Yiqing Li[b,d,*], Yusheng Yang[a,b,**]

[a] State Key Laboratory of Humid Subtropical Mountain Ecology, Fuzhou 350007, China
[b] School of Geographical Sciences, Fujian Normal University, Fuzhou 350007, China
[c] Research Designs/Hubbard Brook Experimental Forest, 56 Horton Lane, Lyme, NH 03768, USA
[d] College of Agriculture, Forestry and Natural Resource Management, University of Hawaii, Hilo, HI 96720, USA

ARTICLE INFO

Keywords:
Cunninghamia lanceolata
Fine root turnover
Interactive effect
Nitrogen deposition
Soil warming
Subtropical plantation

ABSTRACT

Forest aboveground production and soil carbon (C) pools are closely linked to fine root dynamics. Uncertainty about the effects of warming and nitrogen (N) deposition on fine root dynamics limits our ability to predict how C will transfer between biological and atmospheric pools in tropical and subtropical forests. In order to examine the effects of warming and N deposition on fine roots in subtropical plantations, we used a randomized complete block design with factorial soil warming (ambient, ambient + 5 °C) and N deposition (ambient, ambient + 80 kg N ha^{-1} yr^{-1}) manipulation. Minirhizotrons were used to monitor fine root production, mortality and turnover rate of Chinese fir (*Cunninghamia lanceolata*) seedlings for two years, and seedling growth was measured. We found warming had positive effects on annual fine root production, mortality and turnover rate both under ambient and increased N addition. N addition had positive effects on annual fine root production, mortality and turnover rate in the warmed plots, but had no influence on annual fine root production, mortality and turnover rate in the unwarmed plots. Warming and N addition had an additive (not interactive) effect on fine root production, mortality and turnover rate. There was an interaction between warming and N addition on living fine root biomass in the second year. These changes can be largely attributed to belowground/aboveground C allocation. There was no evidence of root respiration acclimation to warming. In addition, increased fine root turnover rate after warming implies accelerated root C inputs to soils, which may affect soil C and nutrient dynamics. Nitrogen addition may exacerbate this. There was no acclimation of root respiration to warming, which may alter C balance and cause more CO_2 release to the atmosphere through autotrophic respiration.

1. Introduction

The impact of climate warming and atmospheric N deposition on patterns and processes of natural forests and plantations has been an important topic in global change studies. However, the majority of manipulative studies on the effects of warming and N deposition were conducted by using either warming or N addition as a treatment (Kern et al., 2004; Mo et al., 2008; Chen and Brassard, 2013; Noh et al., 2016). Because of the co-occurrence of warming and N deposition worldwide, the two major influential global change driver may potentially have interactive effects on forest ecosystem performance and function (Lupi et al., 2012). Therefore, single-factor experiments may be inadequate to fully understand the responses of natural forests or plantations to global warming and N deposition (Dermody et al., 2006). Experiments examining both independent and combined effects of warming and N deposition should be far more informative.

During the past two decades numerous manipulative experiments on the effects of warming or N deposition have been carried out globally (Melillo et al., 2002; Butler et al., 2012; Fan et al., 2015; Hasselquist et al., 2012). However, those studies are mainly concentrated in temperate and boreal regions, with few studies in the tropical and subtropical areas (Zhou et al., 2013; Cavaleri et al., 2015). Tropical and subtropical plant species may be more susceptible to warming than species in temperate or boreal regions as a consequence of millions of years of evolution under relatively narrow temperature variation in the tropics and subtropics (Wright et al., 2009; Krause

* Corresponding author. School of Geographical Sciences, Fujian Normal University, Fuzhou 350007, China.
** Corresponding author. School of Geographical Sciences, Fujian Normal University, Fuzhou 350007, China.
E-mail addresses: yiqing@hawaii.edu (Y. Li), geoyys@fjnu.edu.cn (Y. Yang).

https://doi.org/10.1016/j.soilbio.2018.05.009
Received 30 August 2017; Received in revised form 19 March 2018; Accepted 12 May 2018
0038-0717/

et al., 2013). Compared with temperate and boreal forests, tropical and subtropical forest soils are highly weathered with relatively higher soil N availability (Zhang et al., 2011) and a faster N cycling rate. Thus, the effects of both warming and N deposition on forest ecosystems in the tropics and subtropics could be very different from temperate or boreal forests. Research in tropical and subtropical regions has largely lagged behind despite the fact that these regions are facing substantial increases in both temperature and N deposition (Field et al., 2014; Cavaleri et al., 2015; Kanakidou et al., 2016).

Previous studies have shown that warming and N deposition may directly or indirectly affect above- and belowground processes in forest ecosystems and the consequent responses to the climatic changes (Way and Oren, 2010; Burton et al., 2012; Lu, 2013). Both above- and belowground biomass allocation influences ecosystem function and associated soil carbon input as well as ecosystem carbon cycling (Kuzyakov and Domanski, 2000; Litton et al., 2007). However, the responses of belowground processes, such as fine-root production and turnover rate, have been much less studied than the aboveground processes (Pregitzer et al., 1995; Leppälammi-Kujansuu et al., 2014). Due to the logistical and technical difficulties of fine root extraction and accurate measurement in natural forests and plantations, studies on the effects of warming and N deposition on fine root production, mortality and turnover are extremely limited, especially in the tropics and subtropics (Zhou et al., 2013).

Rhizosphere temperature affects the growth, mortality and turnover of plant roots and consequently influences soil C sequestration and storage (Brunner and Godbold, 2007). To date, research results on the responses of fine roots to warming are inconsistent. For example, King et al. (1999) and Brassard et al. (2009) reported that warming increased the turnover of fine roots in a natural forest but Hollister and Flaherty (2010) and Chen and Brassard (2013) reported that fine root turnover rate was not affected by warming. Eissenstat et al. (2013) found a negative effect of warming on turnover rate of fine roots. The N deposition effects on fine root dynamics appears to have received more attention than warming effects during the past several decades. Some studies found that fine root turnover rate increased with N deposition (Pregitzer et al., 2000; Majdi and Andersson, 2005) but others found it decreased (e.g. Kern et al., 2004). Kang et al. (2016) reported that N deposition did not affect fine root turnover rate. The divergent findings from those studies indicate that the responses of fine root dynamics to N deposition is ecosystem-dependent and that a great deal of uncertainty exists regarding the effects N deposition on fine root dynamics. Previous studies on the effects of warming and N deposition on fine root have mostly focused on individual factors and little attention has been paid to the interaction of warming and N deposition due to cost constraints on this type of environmental research (Zuidema et al., 2013). However, with the increasing warming and N deposition in many regions of the globe, including southeast of Asia, studies on the potential interactive effects of warming and N deposition on root dynamics of natural forests or plantations cannot be neglected anymore (Majdi and Öhrvik, 2004).

Root tissue chemistry and physiology play a key role in controlling the metabolic and decomposition dynamics of roots (King et al., 2005; Zhou et al., 2011). Little information is available on how warming and N deposition will jointly affect the chemistry and physiological characteristics of fine roots, such as N, P, C:N ratio, N:P ratio, soluble sugars, starch and non-structural carbohydrate (NSC) concentration. Yang et al. (2013) reported that increased soil temperature is linked to increased N concentration and N:P ratio in root tissues due to enhanced root activity and N availability at higher temperature. And this may increase the root respiration rate mainly due to it is directly related to tissue N concentration (Pregitzer et al., 1998). It is also of note that roots in warmed soils have a greater respiration rate, which increases the C required for maintenance (Winkler et al., 1996) and may result in more rapid root mortality (Majdi and Öhrvik, 2004). Pregitzer et al. (2000) found that NSC accounted for 4%–23% dry weight of fine roots may act as a marker of the functional response of fine roots for carbon consumption and storage. These compounds constantly provide C and energy for fine root activities and lack of such compounds could lead to dysfunction of fine roots (McDowell, 2011), and these carbohydrate reserves are allocated to compensatory growth when soil temperature increases. Thus, the information on fine root tissue chemistry should provide insight into the understanding the mechanisms of the effects of warming and N deposition on fine root dynamics.

Chinese fir (*Cunninghamia lanceolata*) plantations are the most important commercial timber source in China, accounting for 6% of the world's plantations. They also play an important role in carbon sequestration in China (Piao et al., 2009). To our knowledge, there have been no field experiments for examining the effects of warming and N deposition on fine roots of Chinese fir plantations. In this experiment, using a two-factorial experimental block design combined with minirhizotron techniques and measurements of seedling growth, we examined the effects of soil warming and N addition on fine root production, mortality and turnover rate of Chinese fir. Our goal was to answer the following questions: (1) How will soil warming and N addition affect fine root production, mortality and turnover rate? (2) Are there synergistic effects between warming and N addition on fine roots? (3) How will soil warming and N addition affect the chemical and functional characteristics of fine roots? (4) How does altered belowground C allocation in response to N addition and/or warming effect aboveground productivity?

2. Materials and methods

2.1. Study site description

This study was conducted at Chenda Research Station of Fujian Normal University in Fujian province of China (26°19′N, 117°36′E), the elevation is 300 m above sea level. The study area has a subtropical monsoonal climate with a mean annual temperature of 19.1 °C and a mean annual frost-free period of approximately 300 days. The mean annual precipitation is 1750 mm with 75% occurring from March to August. The mean annual evapotranspiration and relative humidity are 1585 mm and 81% respectively. Evergreen broad-leaved species are the dominant vegetation in the study area. The parent material of the soils is granite and the soils are classified as red and yellow soils according to the China soil classification systems.

2.2. Experimental design

The warming and N addition experiment was established in October 2013. Randomized complete block factorial design was used in this experiment, with warming and N addition as fixed factors. A total of twenty 2 × 2 m plots were assigned to four treatments: control (C), warming (W, +5 °C), nitrogen addition (N, +80 kg N ha^{-1} yr^{-1}), and warming plus nitrogen addition (WN). The experiment was carried out on a flat area which is not significantly affected by hydrological conditions of neighbor forests (Fig. 1). PVC boards with a thickness of 0.8 cm were inserted into the soil at a depth of 70 cm to separate the plots, and the bottom of each plot has not been isolated. In the warming plots, heating cables (Nexans type TXLP, Oslo, Norway) with a heat output of 100 W m^{-2} and a diameter of 6.5 mm were installed at a soil depth of 10 cm with a distance of 20 cm between the cables. Temperatures in the warming plots were targeted at 5 °C higher than the non-warming plots. Cables were installed in the control plots to compensate for potential soil disturbance effects, but they were not turned on.

The temperature was controlled using individual proportional/integral/derivative (PID) controllers for each plot. Plot temperatures were measured with thermistor temperature probes and the plot temperature was set with reference to control-plot thermistors placed in unheated plots. This control method allowed the heated plots to respond quickly